Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus

Rudo von Cosel
Muséum National d'Histoire Naturelle
55 Rue Buffon, F-75005 Paris
FRANCE
cosel@mnhn.fr

Bruce A. Marshall
Museum of New Zealand Te Papa Tongarewa
P.O. Box 467, Wellington
NEW ZEALAND
brucem@tepapa.govt.nz

ABSTRACT

Two new species and a new genus of large mussels from off northern New Zealand are described. *Bathymodiolus tangaroa* new species from seeps (presumably methane-rich) off Cape Turnagain and Cape Kidnappers at 920–1205 m, and *Gigantidas gladius* new genus and new species from active submarine volcanoes on the southern Kermadec Ridge at 216–755 m. *Gigantidas gladius* is anatomically closer to the small, wood-associated species of *Idas* Jeffreys, 1876, than to any of the large mussels currently known from hydrothermal vents or seeps. A polychaete of the genus *Branchipolynoe* Pettibone, 1984, was found within the mantle cavity of every specimen of *Gigantidas gladius*

INTRODUCTION

Following the discovery of a number of species of large mussels associated with seeps and hydrothermal vents from the eastern Pacific, Japan, Fiji, the Caribbean, the Gulf of Mexico, and the Mid-Atlantic Ridge (Kenk and Wilson, 1985; Cosel et al., 1994; Hashimoto and Okutani, 1994; and references therein), examples of a related species were obtained by commercial fishing at two sites off the east coast of the North Island of New Zealand (Lewis and Marshall, 1996) (Figure 1B). This mussel, here referred to as the genus *Bathymodiolus* Kenk and Wilson, 1985, occurs on slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate.

A second, much larger species was obtained subsequently by dredging during surveys of active submarine volcanoes present along the southern Kermadec Arc off northeastern North Island (Parson and Wright, 1996; Wright, 1994, 1997; de Ronde et al., 2001; and references therein) by the National Institute of Water and Atmospheric Research, Wellington (Figure 1C).

Institutional abbreviations used in the text are: MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; NIWA, National Institute of Water and Atmospheric Research, Wellington.

SYSTEMATICS

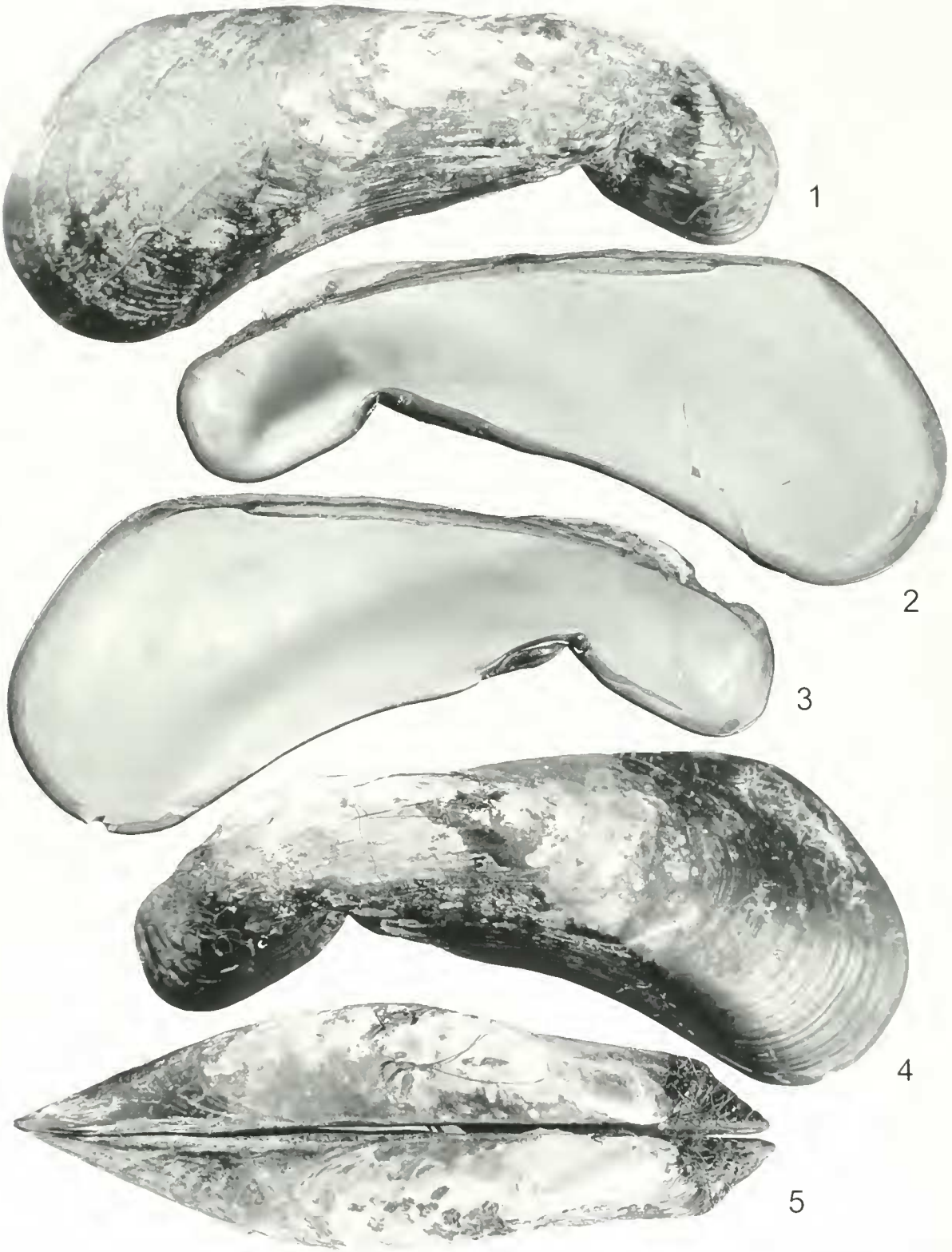
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Genus *Bathymodiolus* Kenk and Wilson, 1985

Bathymodiolus Kenk and Wilson, 1985: 255. Type species (by original designation): *Bathymodiolus thermophilus* Kenk and Wilson, 1985; Recent, Galapagos Rift.

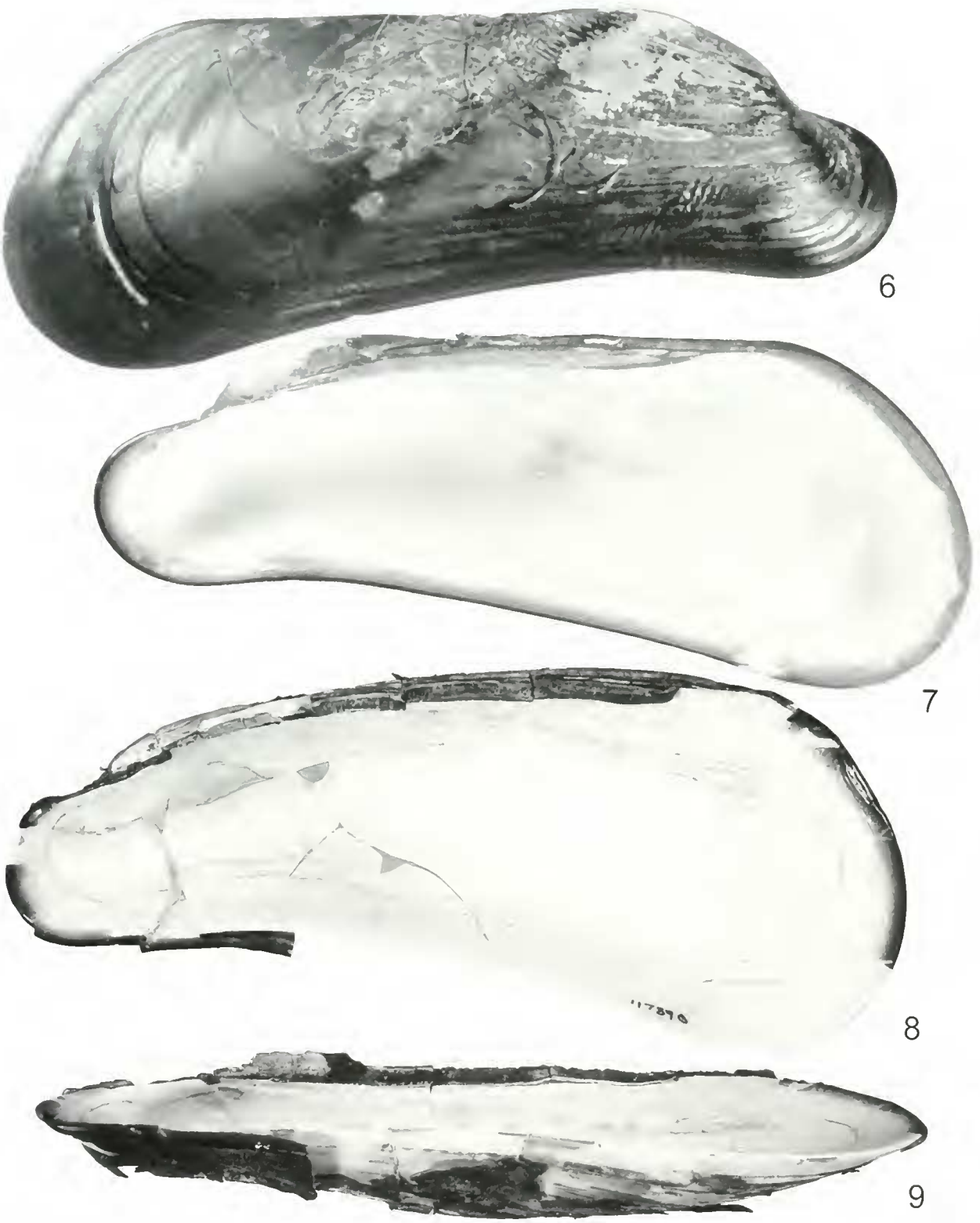
Bathymodiolus tangaroa new species
(Figures 1–13, 15–18, Table 1)

aff. *Bathymodiolus* sp.—Lewis and Marshall, 1996: 183; 186, fig. 4, 1B7
Bathymodiolus sp.—Cosel and Olu, 1998: 658.
Bathymodiolus sp. H—Cosel, 2002: table 1

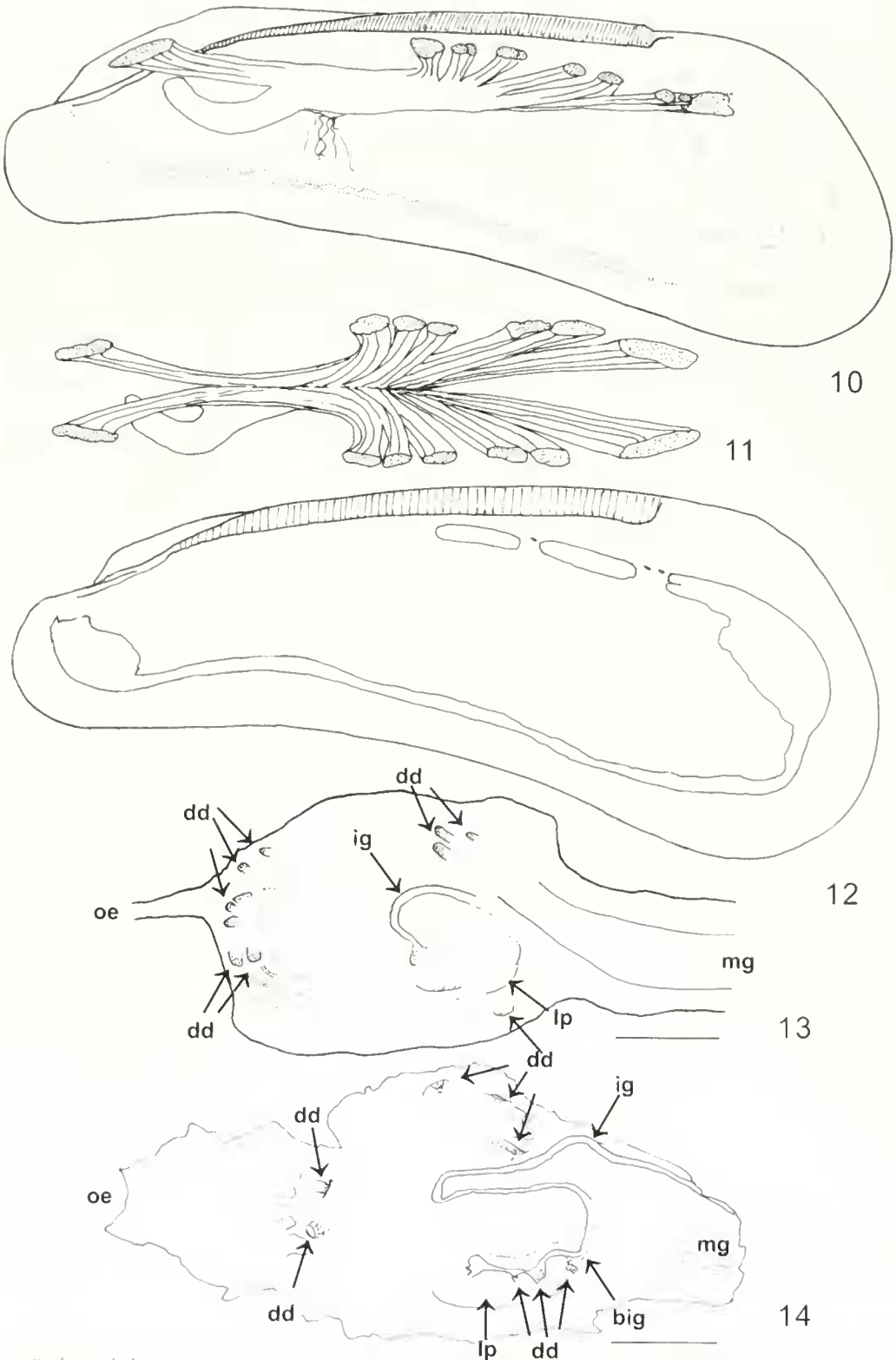
Description: Shell large, up to almost 200 mm long, elongate, somewhat aduliform, rather thick and solid, externally with well-developed, irregular growth lines; dull-whitish beneath periostracum; internally nacreous-ivory. Beaks subterminal, at about one-seventh total shell length in adults; umbones very broad, flattened. Height gradually increasing posteriorly, markedly curved dorso-ventrally, most inflated at about mid-length, equivalve, length/height ratio 2.3–3.2. Few specimens somewhat twisted. Anterior part short, rather narrow, protruding nose-like anteriorly; anterior margin narrowly but evenly rounded; ventral margin markedly concave over anterior half. Posterior margin evenly rounded ventrally, convex dorsally; postero-dorsal angulation well-defined, rounded, situated above posterior adductor scar, close to posterior margin. Prodissoconch unknown. Periostracum thick, hard, dark brown, smooth, glossy to somewhat dull, no periostracal hairs (byssal endplates of other specimens scattered over valves). Hinge (adults) toothless, anterior hinge margin weakly protruding ventrally. Ligament opisthodetic, very strong, extending over



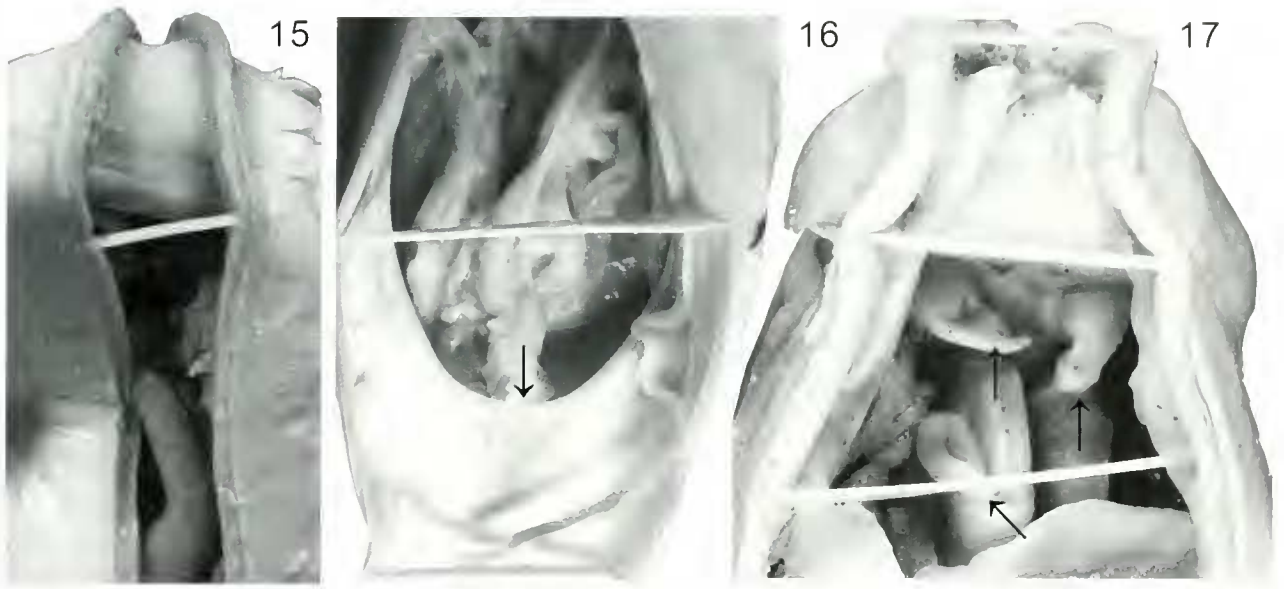
Figures 1–5. *Bathymodiolus tangaroa* new species. Holotype, Madden Basin, shell length 199.6 mm, NMNZ M. 158284. **1, 2.** Exterior and interior of right valve. **3, 4.** Interior and exterior of left valve. **5.** Dorsal view.



Figures 6–9. *Bathymodiolus tangaroa* new species. **6, 7.** Paratype 5, Madden Basin (shell length 110.5 mm, NMNZ M.158227, 5). Exterior and interior of right valve. **8, 9.** Paratype 3, Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). Lateral and oblique ventral view of interior of right valve, with muscle scars and pallial line highlighted.



Figures 10–14. *Bathymodiolus tangaroa* new species and *Gigantidas gladius* new species, half-schematic drawings. **10, 11.** *Bathymodiolus tangaroa*, paratype 3, off Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). **10.** Sketches of foot-byssus retractor complex in left lateral (10) and dorsal (11) view and its situation in the shell. **12.** *Bathymodiolus tangaroa*, paratype 5, off Cape Kidnappers (shell length 161.3 mm, MNHN). Interior of right valve, showing muscle scars and pallial line. **13.** *Bathymodiolus tangaroa*, paratype 1, Madden Basin (shell length 177.9 mm, NMNZ M.158227/8). Dorsally opened stomach (scale bar = 5 mm). **14.** *Gigantidas gladius*, paratype 3, Rumble V (shell length 271.3 mm, NMNZ M.154988/3). Dorsally opened stomach (scale bar = 5 mm). (big, beginning of intestinal groove; dd, digestive diverticula duct (entrance); ig, intestinal groove; lp, left pouch; oe, esophagus).



Figures 15–17. *Bathymodiolus tangaroa* new species. **15, 16.** Paratype 3, Cape Kidnappers (shell length 167.8 mm, NMNZ M.117890/3). **15.** Ventral view of anterior end, showing thin, transverse part of inner mantle fold, and ventrally grooved foot. **16.** Ventral view of posterior end, showing valvular siphonal membrane (arrow) without median papilla. **17.** Paratype 6, Cape Kidnappers (shell length 160 mm, NMNZ M.117890/6). Ventral view of anterior end, showing labial palps (arrows).

about five-sixths of postero-dorsal margin in front of postero-dorsal corner, and ending abruptly posteriorly; ligament plate weakly to strongly convex. Subligamental shell ridge well developed, in some specimens divided into a secondary ridge that extends from under umbo for about a third of ligament length; primary ridge extending posteriorly behind umbo, between ligament and secondary ridge, and becoming obsolete shortly before posterior end of ligament (visible only from ventral perspective). Adductor scars well defined. Anterior adductor scar short, situated just in front of umbo. Posterior adductor scar rather large, more or less rounded, united with most posterior scar of posterior pedal and byssus retractor muscle complex; anterior scar of this complex well separated, very long and itself divided into isolated impressions, extending posteriorly from under middle of ligament. Anterior byssus retractor muscle scar situated deep under beak on anterior part of umbonal cavity (visible only from ventral perspective). Pallial line curving parallel to ventral margin.

Anatomy: Ctenidia long, narrow, about 75% of shell length (125 mm long and 13 mm wide in 167 mm specimen), outer and inner demibranchs of equal length, filaments broad and fleshy, food-groove not detected (probably because of poor fixation). Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance, those of inner demibranch fused to visceral mass. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, nor connection bars between free edges and gill axes. Inner mantle folds separate along entire ventral margin length from anterior adductor to posterior margin; edges slightly frilled over most of length, more undulate along posterior 30–50 mm; terminating anteriorly over anterior adductor, folded back directly onto muscle and continuing over it as a thin, delicate, inconspicuous membrane. Valvular siphonal membrane short and thin, without median papilla. Foot-byssus retractor muscle complex moderately elongate; anterior retractor rather short, very broad, inserted in anterior part of long umbonal cavity, most anterior point under beaks (larval shell). Posterior byssus retractor comprising several diverging muscle bundles with common base at base of byssus; anterior part comprising 3 bundles attached to very long scar at about middle of valves, at about a right angle (most anterior bundle) and about 80 and 60° to longitudinal shell axis (second and third bundle); posterior part consisting of 4–5 bundles passing towards 2 attachment points, most posterior bundle just before posterior adductor. Posterior foot retractor long and thin, arising from anterior side of base of foot behind base of anterior retractor muscles, passing parallel to longitudinal shell axis towards anterior bundle of posterior byssus retractor, then bent dorsally to attachment point, where closely appressed to anterior bundle of posterior byssus retractor. Foot relatively small, 35 mm long (byssal orifice included) in a specimen of 167 mm shell length. Two pairs of labial palps present, anterior pair relatively small, posterior pair long and narrowly triangular (respectively 7 mm and 12–13 mm long in a 160 mm specimen). Intestinal tract narrow. Stomach situated just behind middle of anterior half of shell length, simple, thin-walled, anterior chamber ill-defined, posterior chamber longer. Divertienlar entrances 13, 7 in anterior chamber, and 6 in posterior chamber. Depression on posterior left side corresponds to left ponch. Midgut

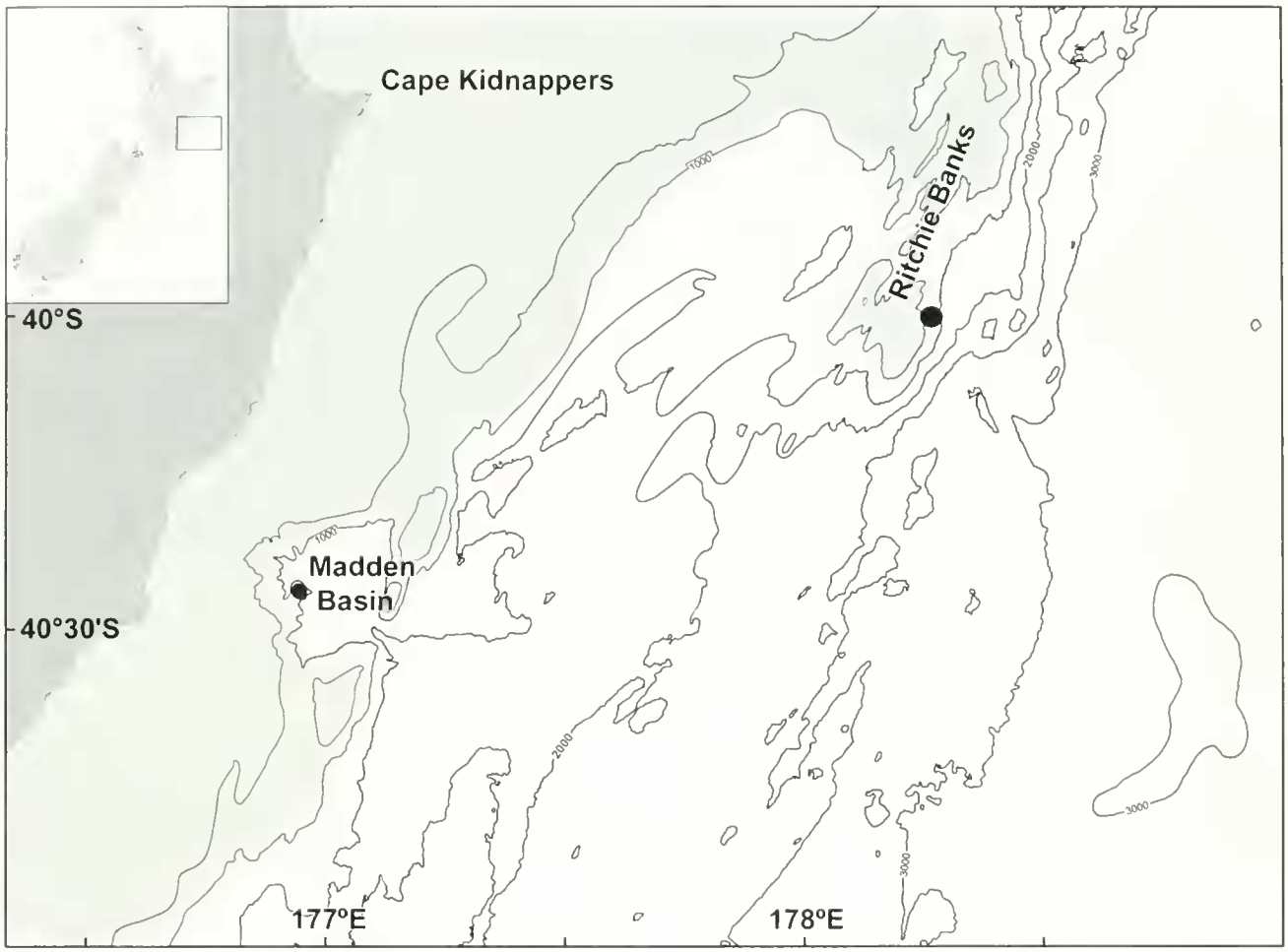


Figure 18. Bathymetric chart of eastern central North Island showing localities for *Bathymodiolus tangaroa* new species. Isobaths at 1000 m intervals, seafloor shallower than 1000 m shaded. Base map courtesy NIWA (adapted).

running posteriorly straight and medially from the stomach, under ventricle and entering ventricle just in front of ostia, without any loop or curve; behind heart, intestine passing over posterior adductor and ventrally on its posterior side; anus at mid-diameter of posterior adductor. Heart rather broad, situated in the posterior half of shell length, anterior extremity of ventricle at mid-shell/mantle length. Auricles long, fused posteriorly just in front of the posterior adductor, and stretching out forward in narrow lobes to the anterior bundle of the posterior retractor.

Table 1. *Bathymodiolus tangaroa* new species. Shell measurements (mm) and proportions. Paratypes 3, 5 and 6 from off Cape Kidnappers, others from type locality.

Length	Height	Tumidity	Length/height	Specimen
199.6	71.1	61.2	2.69	Holotype NMNZ
177.9	58.6	50.6	3.03	Paratype 1 MNHN
171.0	58.0	52.5	2.95	Paratype 2 NMNZ
167.8	52.6	53.6	3.19	Paratype 3 NMNZ
162.0	62.0	49.0	2.61	Paratype 4 NMNZ
161.3	63.6	50.7	2.54	Paratype 5 MNHN
160.0	56.6	52.0	2.83	Paratype 6 NMNZ
148.5	53.8	45.5	2.76	Paratype 7 NMNZ
110.5	41.6	37.3	2.66	Paratype 8 NMNZ
103.0	38.6	34.7	2.67	Paratype 9 NMNZ
101.7	40.5	36.8	2.51	Paratype 10 NMNZ

Type Material: Holotype (pair) NMNZ M.158284, and 8 paratypes (6 pairs NMNZ M.158227, 1 pair NIWA P1291, 1 pair MNHN); from type locality, alive, 26 May 2001, FV Tasman Viking (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), presented by S. Donker. Paratypes: South Ritchie Bank, SE of Cape Kidnappers, North Island, New Zealand, 40°00.8′ S, 178°16.0′ E, alive, 1170 m, 1994, FV San Manukai (semi-pelagic "orange roughy" trawl that accidentally engaged bottom), leg. M. Friar (paratypes 3 and 6, pairs, NMNZ M.117890; paratype 5, pair, MNHN).

Type Locality (Figure 18): South side of Madden Basin, off Cape Turnagain, eastern coast of North Island, New Zealand, 40°26.49′ S, 176°58.13′ E, 920–1205 m.

Distribution (Figure 18): Off southeastern North Island, New Zealand, living at 920–1205 m.

Biotope: On hard bottom on the slope ridges landward of the accretionary prism of the convergent Pacific-Australian plate, where plumes of sonar-reflective water, presumably rich in hydrocarbons, rise from the seabed (for details, see Lewis and Marshall, 1996) (Figure 18). We presume that the mussels live at these emission sites and are nourished by methane-metabolizing symbiotic bacteria concentrated in their enlarged gills (Childress et al., 1986; Fisher et al., 1987; Tunnicliffe, 1991; Rio et al., 1992; and references therein).

Etymology: Named after the Maori sea god *Tangaroa*.

Remarks: *Bathymodiolus tangaroa* is strongly characterized by its markedly curved shell and distinctively elongate-cuneiform outline; no other species has this shape. *Bathymodiolus heckerae* Gustafson et al., 1998, from the Gulf of Mexico, is of similar size range but more slender and less curved, with thinner-walled valves. *Bathymodiolus boomerang* Cosel and Olu, 1998, from the Barbados Accretionary Prism, is thinner-walled, more elongate, and considerably larger. *Bathymodiolus brevior* Cosel et al., 1994 (Lau Basin and North Fiji Basin), *B. puteoserpentis* Cosel et al., 1994 (Mid-Atlantic Ridge), and *B. marisindicus* Hashimoto, 2001 (Rodriguez Triple Junction), are shorter and stouter than *B. tangaroa*, with a markedly broader anterior margin. *Bathymodiolus childressi* Gustafson et al., 1998, from the Gulf of Mexico has the cuneiform shape of *B. tangaroa*, but is much shorter with almost terminal umbones.

Bathymodiolus tangaroa differs from *Bathymodiolus* species for which anatomy is known in that the inner mantle fold is much thinner, more delicate, and less conspicuous where it extends transversally over the anterior adductor. *Bathymodiolus tangaroa* differs further from all species other than the group comprising *B. childressi*, *B. platifrons* Hashimoto and Okutani, 1994, *B. mauritanicus* Cosel, 2002, and an undescribed species from Barbados (currently under study by R. v. C.), by its multi-bundle foot-byssus-retractor complex. The posterior retractor in *B. tangaroa*, however, is much longer than the anterior one, rather than *vice versa* as in *B. childressi* (see Gustafson et al., 1998: 77, fig. 13) and the undescribed species from Barbados (condition unknown in *B. platifrons* and *B. mauritanicus*). Another common feature of *B. childressi*, the undescribed Barbados species, and *B. tangaroa* is the lack of a papilla in the middle of the posterior of the valvular siphonal membrane. Thus *B. tangaroa* cannot be assigned to any of the four informal subgroups of *Bathymodiolus* defined by Cosel (2002), specifically the *B. thermophilus* group (one species), the *B. brevior* group (five species), the *B. heckerae* group (two species) and the *B. childressi* group (four species).

Of the 11 specimens examined, one (length 177.9 mm, paratype MNHN) contained a polychaete worm of the genus *Branchipolynoe* Pettibone, 1984 (length 32.5 mm), which was situated in the mantle cavity above the byssus.

Gigantidas new genus

Type Species: *Gigantidas gladius* new species; Recent, New Zealand.

Diagnosis: Shells attaining very large size (length up to 316 mm), extremely slender. Umbones at about 20% of total shell length. Juveniles (<5 mm) with periostracal bristles. Animal with very long, rather narrow, fleshy ctenidia. Inner mantle folds entirely separate, terminating anteriorly over anterior adductor, edges frilled along posterior 3/4 of shell length. No valvular siphonal membrane. Inner mantle folds below posterior adductor with a deep cleft between left and right mantle lobes. Foot very small, anterior retractor inserting on shell directly above anterior adductor, well in front of umbonal cavity, both muscles forming a common scar.

Remarks: The large size and biotope of *Gigantidas gladius* invites immediate comparison with large mussels of the genus *Bathymodiolus*, from all of which, however, it differs by the absence of a well-developed valvular siphonal membrane at the posterior end, and the absence of a continuation of the inner mantle fold across the anterior adductor from one valve to the other. Moreover, unlike *Bathymodiolus* species, the attachment point of the anterior retractor is not situated somewhere within the umbonal cavity but well in front of it, on the narrow anterior part of the valves close to the antero-dorsal margin. In *Bathymodiolus*, the anterior adductor and retractor muscles are situated close together at their attachment point, especially in species with terminal umbones, but remain well separated through ontogeny (Figure 10; see also Cosel et al., 1999: figs. 12, 13, 22, 59, 60, 61). In *Gigantidas gladius* both muscles are in contact at their insertion point and form a common scar. Very young specimens of *G. gladius* have periostracal bristles on the postero-dorsal part, whereas these have never been recorded from *Bathymodiolus* species at any stage of growth (e.g. Cosel et al., 1994; Hashimoto and Okutani, 1994; Cosel and Olu, 1998; Cosel et al., 1999).

The attachment point of the anterior retractor in very young specimens of *G. gladius* (<5 mm) is in the umbonal cavity as in adult *Bathymodiolus* species, but with increasing shell size it progressively shifts anteriorly from the anterior part of the umbonal cavity to a position under the antero-dorsal margin, remaining very close to the anterior adductor throughout ontogeny. The only other large mussel known in which the anterior retractor scar is situated in front of the umbonal cavity closely adjacent to the anterior adductor scar, is an undescribed species from the Kaikata Seamount, Japan. According to Hashimoto and Horikoshi's (1989) illustration, the retractor scar in the Japanese species is very close to the adductor scar but not in contact with it, and the two bundles of the posterior retractor are well separated. The Japanese

species, which may thus belong in *Gigantidas*, is smaller and more strongly curved than *G. gladius*, and was found burrowing in sediment on a dormant submarine volcano.

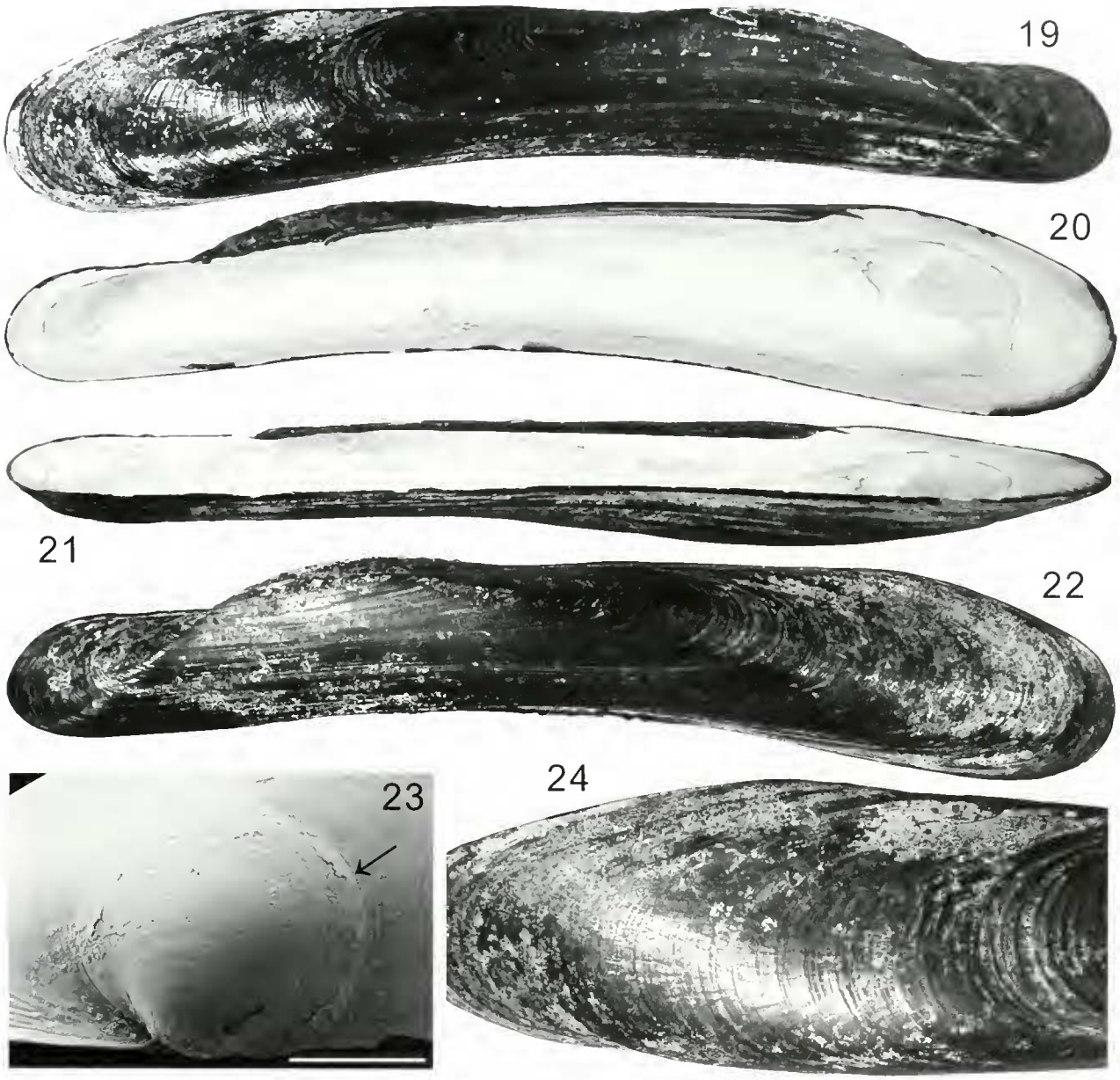
Anatomically, *G. gladius* most closely resembles the much smaller mussels of the genus *Idas* Jeffreys, 1876 (type species *I. argenteus* Jeffreys, 1876; North Atlantic) (*I. japonica* up to 8.9 mm long), which live at similar depths associated with decaying wood and whale bones, and *Benthomodiolus* Dell, 1987 (type species *B. lignicola* Dell, 1987; New Zealand) (length up to 17.3 mm), which lives on decaying wood. In the absence of animals of the type species of *Idas* for comparison, we have had to base our comparison on specimens of the New Zealand *Idas* species identified by Dell (1987) as *I. japonica* (Habe, 1976) (NMNZ M.75022). This species and *G. gladius* share a similarly-shaped posterior end of the inner mantle fold, with a short, narrow, deep cleft between the left and right mantle lobes, and no valvular siphonal membrane; and lack of tubular prolongation of the exhalent siphon. Periostracal bristles are present in both species, though only in juveniles of *G. gladius*. *Benthomodiolus lignicola* and *G. gladius* both have periostracal bristles, and lack a valvular siphonal membrane, and a tubular prolongation of the exhalent siphon. *Gigantidas* thus differs from *Idas* primarily in the exceptional size and the biotope of the type species, and in the migration of the insertion of the anterior retractor to a position in front of the umbones.

Species of *Adipicola* Dautzenberg, 1927, which attain up to 31.3 mm in length, are also similar in gross facies. Since soft parts of the type species (*Modiolarca pelagica* Woodward, 1854) were not available for study, we used New Zealand species referred there by Dell (1987, 1995), for comparison, notably *A. arcuatilis* Dell, 1995, a species with a slender, curved shell, living on whale bones. In contrast to *G. gladius*, the inner mantle folds of *A. arcuatilis* are much thinner and less frilled, but at the posterior end, especially over the posterior adductor, they are much more broadened to form a long, thin lobe that extends posteriorly below the exhalent siphon. In contrast to the conditions in *I. japonicus* and *G. gladius*, a valvular siphonal membrane is present in *A. arcuatilis*, but reduced to a narrow, transversely very short rim without a papilla. Moreover, *A. arcuatilis* has a long, tubular exhalent siphon and no periostracal bristles at any stage of growth. *Adipicola osseocola* (also associated with whale bones) lacks periostracal bristles too, and has a tubular exhalent siphon, though shorter than in *A. arcuatilis*.

From the sum of similarities and differences, we conclude that there is a close relationship between *Gigantidas*, *Idas*, and *Benthomodiolus*, that *Adipicola* has closer affinities with *Bathymodiolus*, and that all of these genera form a single phylogenetic radiation within the Mytilidae.

Gigantidas gladius new species
(Figures 14, 19–43; Tables 2, 3)

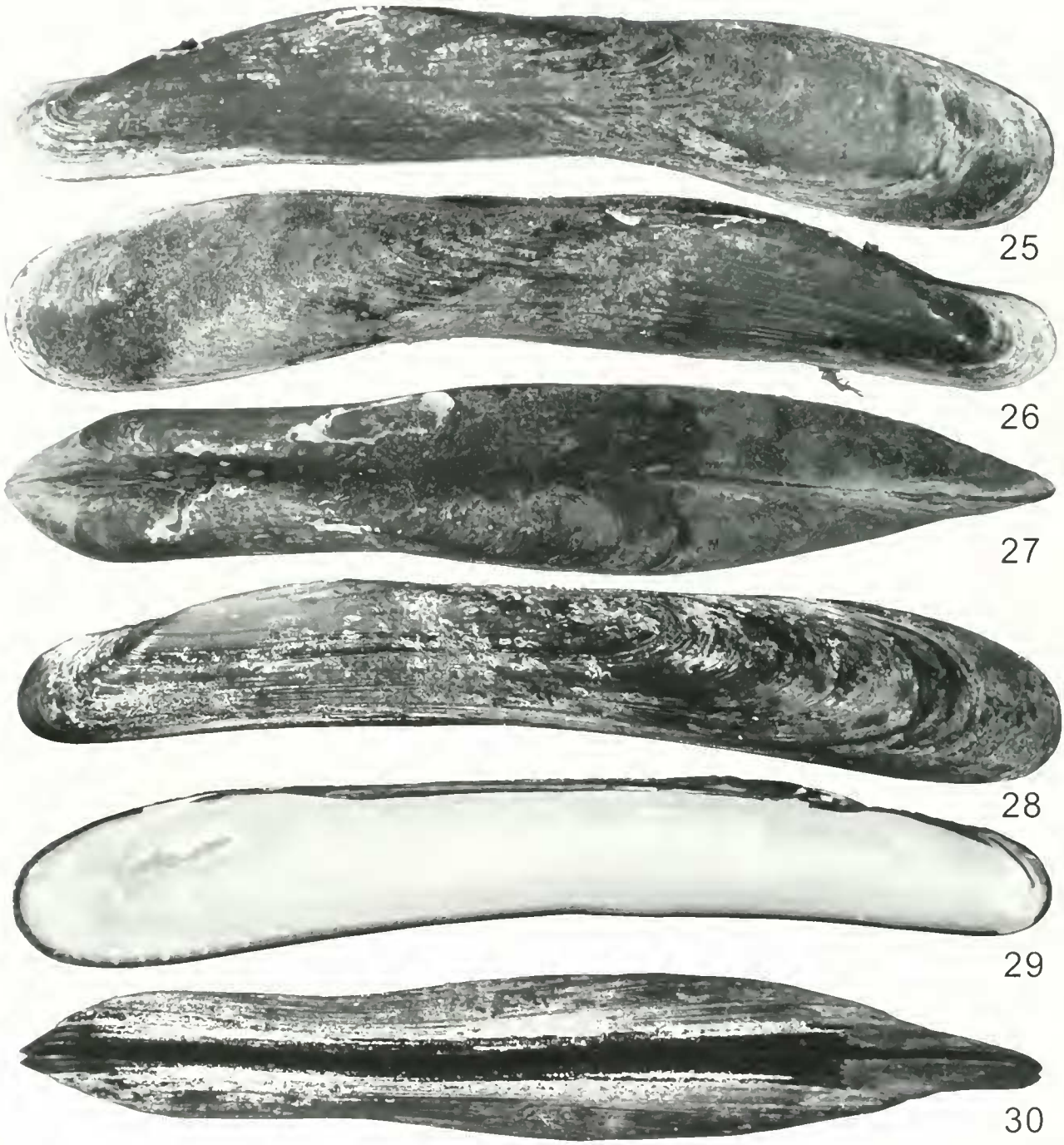
Description: Shell exceptionally large for a mussel, up to 316 mm long, 54 mm high and 56 mm broad, extremely long and slender, rather thin for the size but solid, dull-whitish beneath dark periostracum, interior nacreous-white. Outline somewhat variable, irregular, fully grown specimens elongate-aduliform or bean-shaped, slightly curved dorso-ventrally, most inflated about middle or shortly behind it, equivalve, length/height ratio 4.7–6.2. Half-grown specimens already slender and bean-shaped, very young (length <60 mm) specimens more or less straight. Beaks in adult specimens at about anterior quarter. Anterior part narrow, strongly protruding anteriorly; anterior margin narrowly rounded, ventral margin straight to very slightly concave over anterior half, middle zone of ventral margin markedly concave, straight posteriorly, and slightly convex in posterior fifth. Posterior margin broadly rounded, postero-dorsal margin weakly convex; postero-dorsal corner broadly rounded or not defined, highest part of the valve situated there. Exterior dull, with well-developed, irregular commarginal growth lines. Rounded, pronounced posterior angulation running from umbones towards ventral part of posterior margin, but becoming obsolete on flattened and broader posterior part situated at about 1/7th of shell length. Similar but much shorter anterior angle from umbo to ventral part of anterior margin. Umbones extremely elongated, rather prominent. Fine radial striae running from beaks to anterior, ventral and postero-ventral margins, visible mostly on ventral part of valves, sometimes slightly changing direction at commarginal growth lines. Radial striae weakly reflected on shell interior, mostly ventrally. On postero-dorsal slope striae replaced by low, broad longitudinal waves that bifurcate towards both dorsal margin and posterior angle (Figure 35). Posterior angle smooth. In dorsal or ventral view, broadest part of shell formed by posterior angle. Second broadest part at anterior angle; section under umbones between anterior and posterior angle about same width as anterior angle, in large specimens even slightly constricted there (Figure 27). In some specimens whole shell often more or less spirally twisted. Ligament plate almost straight to slightly convex. Periostracum strong, dark brown, umbonal region and area under umbones light brown, glossy to somewhat dull, smooth; very young specimens (3–6 mm), however, with short periostracal bristles (byssal endplates of other specimens commonly scattered over surface of valves). Hinge in very young specimens (up to about 5 mm long) with row of small denticles of similar size, extending posteriorly from ligament to postero-dorsal angulation, toothless in larger specimens. Anterior hinge margin hardly protruding towards ventral, if at all. Ligament opisthodetic, strong, extending almost over whole of postero-dorsal margin and ending posteriorly 10–20 mm (specimens 200–270 mm shell length) in front of postero-dorsal corner, either abruptly or in a rather short



Figures 19–24. *Gigantidas gladius* new species. **19–22, 24.** Holotype, Rumble V (shell length 260 mm, NIWA H. 790). **19–21.** Exterior, interior and oblique ventral views of right valve. **22.** Exterior of left valve, muscle scars and pallial line highlighted. **24.** Close-up view of posterior part of right valve to show sculpture. **23.** Prodissoconch of juvenile paratype from Rumble III (NMNZ M. 158283). Prodissoconch I and II boundaries arrowed (scale bar = 200 mm).

taper. Subligamental shell ridge well developed from under umbones to about one-half of ligament length, then becoming gradually obsolete, visible under the beaks only from ventral perspective. Adductor scars clearly defined. Anterior adductor scar rather large, arched, situated well in front of umbo, near antero-dorsal margin, united with anterior retractor muscle scar. Posterior adductor scar large, rounded to subangular, united with posterior scar of posterior pedal and byssus retractor muscle scar. Anterior scar of posterior retractor well separated, situated between third and last quarter of ligament length. Anterior byssus retractor muscle scar directly above anterior adductor scar and united with it, well in front of umbones. Pallial line almost parallel to ventral margin. Prodissoconch with glossy, ovate, pinkish purple, sharply delineated, prodissoconch I 83–100 µm wide, prodissoconch II 430 µm wide (development planktotrophic).

Anatomy: Ctenidia very long and narrow, length more than 75% of shell length (78% in shell 271 mm long, 84% in 316 mm specimen); 14 mm broad (outer demi-



Figures 25–30. *Gigantidas gladius* new species. **25–27.** Paratype 1, Rumble III, shell length 316 mm, NMNZ M. 154988/1. **25.** Exterior of left valve. **26.** Exterior of right valve. **27.** Dorsal view. **28–30.** Paratype 3, Rumble V, shell length 271.3 mm, NMNZ M. 154988/3. **28, 29.** Exterior and interior of left valve. **30.** Ventral view.

branchs in a 270 mm specimen; outer and inner demibranchs of equal length, filaments broad and fleshy. Ascending lamellae of outer demibranch anteriorly fused to mantle for a very short distance (about 5 mm), those of inner demibranch fused to visceral mass. Ventral edge of each demibranch with a well-marked food-groove, broader on inner demibranch. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of the ascending lamellae attach, and no connection bars between free edges and gill axes. Inner mantle folds separate along whole length of ventral margin from anterior adductor to posterior margin, their edges frilled along posterior fifth of shell length or even less, becoming smooth towards anterior, terminating anteriorly over an-

Figures 31–38. *Gigantidas gladius* new species, half-schematic drawings. **31–33.** Paratype 3 (shell length 271.3 mm, NMNZ M.154988/3). **31–32.** Sketches of foot–byssus retractor complex in left lateral (31) and dorsal (32) view and its situation in the shell. **33.** Interior of right valve showing muscle scars and pallial line. **34.** Paratype 11 (shell length 206.5 mm, NMNZ M.154988/11). Interior of right valve showing muscle scars and pallial line; location of concealed anterior bundles arrowed. **35.** Paratype 7 (shell length 245.5 mm, NMNZ M.154988/7). Exterior of left valve showing orientation of fine sculpture. **36–38.** Right valves of juvenile paratypes, Rumble III, lengths 72.8 mm (36), 39.8 mm (37) and 34.7 mm (38), NMNZ M.158285.

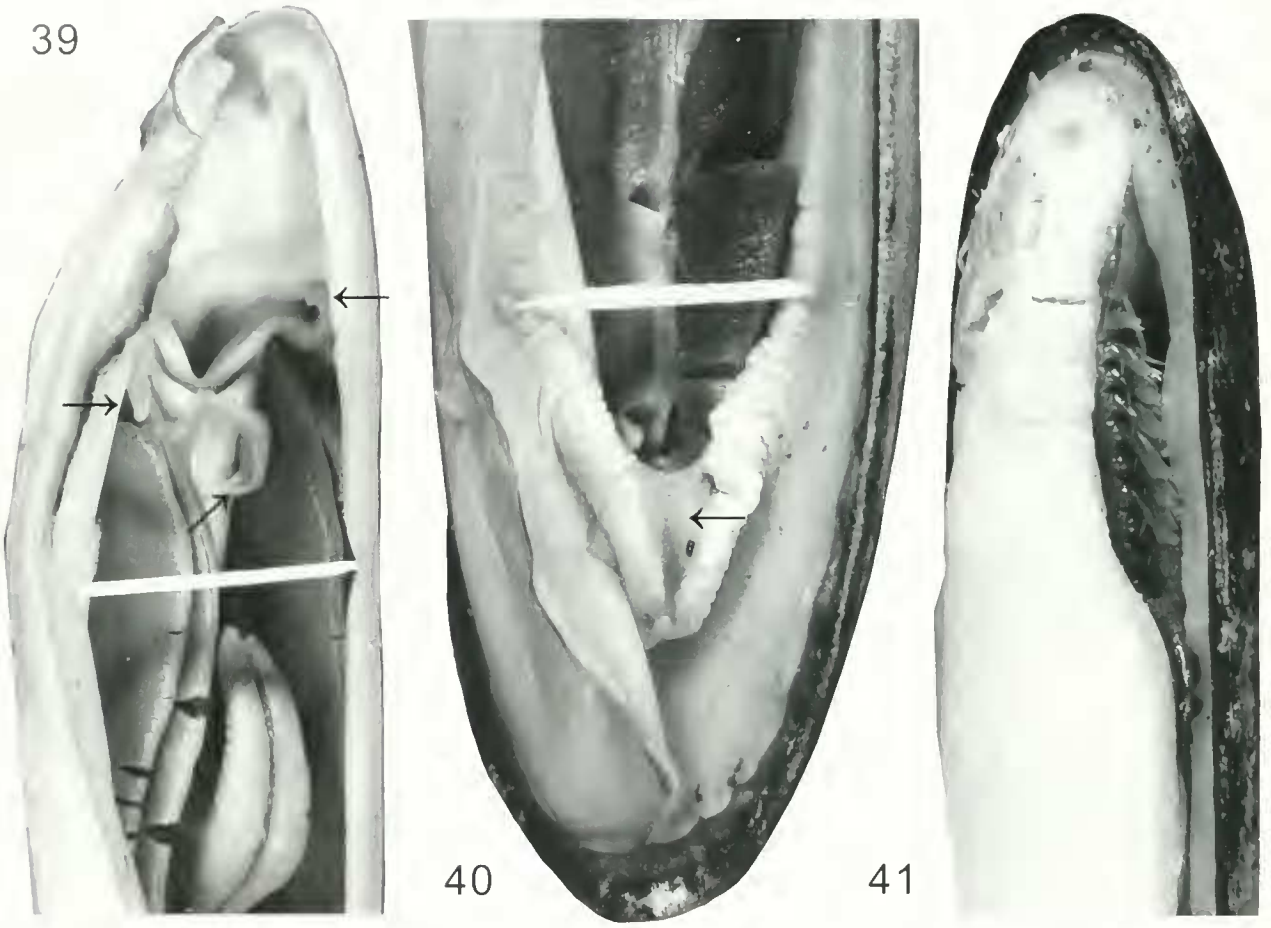


Figure 39–41. *Gigantidas gladius* new species. **39.** Paratype 11, Rumble V (shell length 206.5 mm, NMNZ M.154988/11). Ventral view of anterior end showing mantle edge, anterior and posterior labial palps (arrows), enlarged gills, ventrally-grooved foot, and absence of transverse part of inner mantle fold. **40.** Paratype 9, Rumble V (shell length 231.2 mm, MNHN). Ventral view of posterior end showing muscular connection, cleft posteriorly (arrow) and with vestige of valvular siphonal membrane anteriorly. **41.** Parasitic worm Branchipolynoe sp. (length 34 mm) in situ with associated lesion on anterior mantle edge of paratype 9 of *G. gladius* (shell length 231.2 mm, MNHN).

terior adductor and folding back directly onto adductor but not continuing transversally over it as a rim to meet mantle fold of opposite side. Valvular siphonal membrane absent; however, inner mantle fold folded ventrally and becoming very strong and strongly frilled, with a deep cleft between those of right and left valve. Foot very small: length 34 mm (byssus orifice included) in a specimen of 270 mm shell length. Foot-byssus retractor muscle complex extremely elongated, but anterior retractor rather short. Anterior retractor in adults inserting immediately above anterior adductor, near antero-dorsal margin and well in front of umbonal cavity. In very young specimens (<5 mm long) attachment point is well within anterior part of umbonal cavity though still close to anterior adductor, attachment point migrating anteriorly with increasing size. Posterior byssus retractor comprising 2 principle diverging muscle bundles with common base at base of byssus; anterior bundle broadest, descending at a very low angle to longitudinal shell axis from attachment point at about mid-shell length, posterior bundle thinner, extremely long, extending about parallel to longitudinal shell axis to attachment point just in front of posterior adductor. Two additional very thin bundles attached between anterior and posterior bundles; attachment points varying somewhat from specimen to specimen. Posterior foot retractor very long, passing from anterior side of foot base, behind base of anterior retractor muscles, towards anterior bundle of posterior byssus retractor, reaching attachment point closely appressed to bundle for only a very short part of its length. Labial palps irregular, narrow-triangular, very small in adult specimens (anterior palps 2–5 mm long and posterior pair about 8 mm long in a 270 mm specimen), relatively slightly larger in juvenile and half-grown specimens (posterior palps about 3.5 mm long in a 77 mm specimen). Intestinal tract narrow. Stomach situated between first and second quarters of shell length, small in relation to shell size, rather simple, thin-walled, with a small, rather poorly defined anterior chamber; posterior chamber longer and broader; S di-

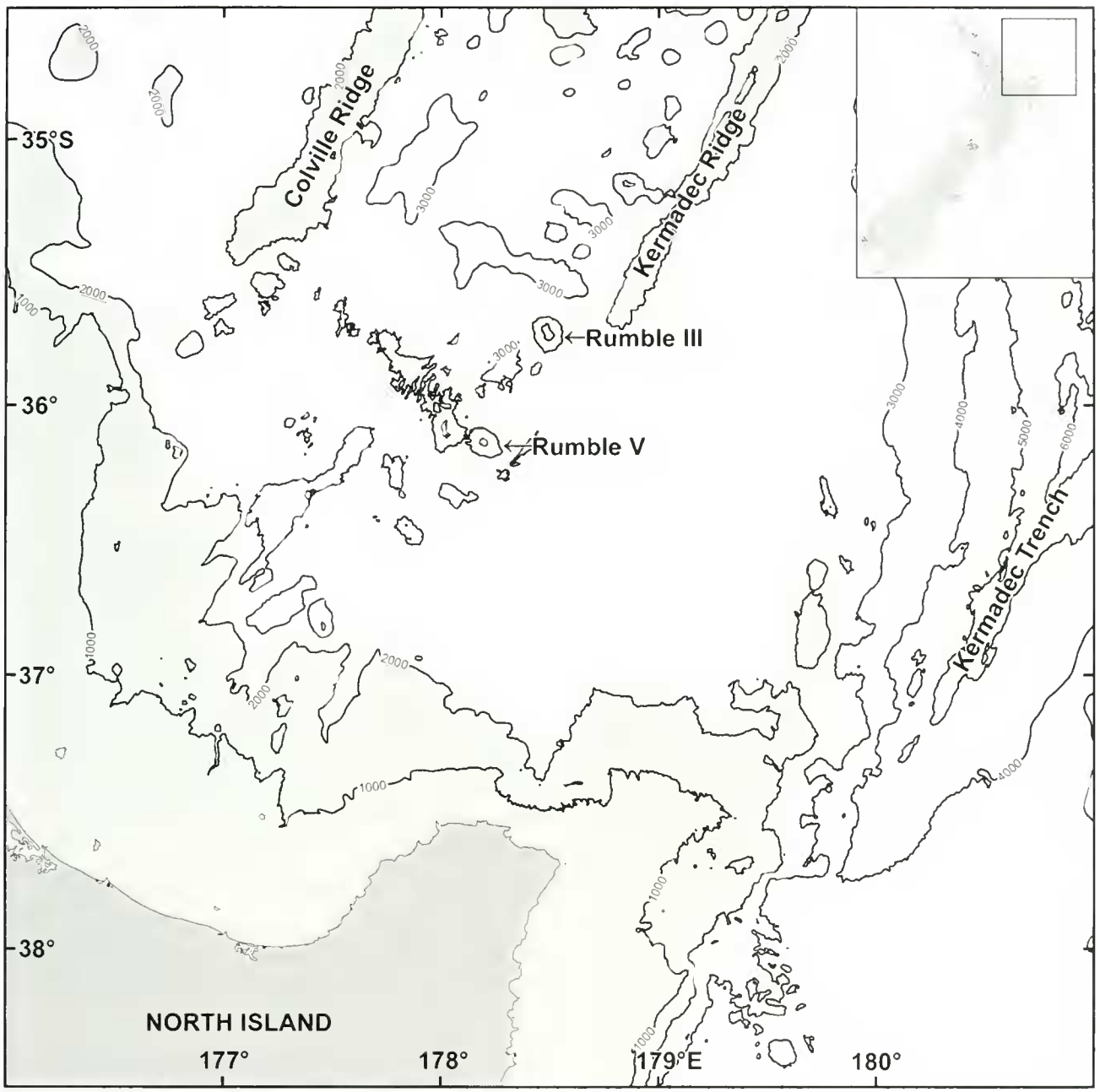


Figure 42. Bathymetric chart showing locations of Rumble III and Rumble V submarine volcanoes, collecting sites for *Gigantidas gladius* new species. Isobaths at 1000 m intervals, seafloor 2000 m and shallower shaded. Base map courtesy NIWA (adapted).

gestive diverticulum entrances visible, 3 at end of anterior chamber, 5 in posterior chamber (specimen examined contained mucus only). Style sac and midgut conjoined. Major typhlosole passing from midgut along floor of posterior chamber to somewhat behind anterior chamber; shallow depression corresponding to left pouch on posterior left side. Gastric shield not detected. Midgut extending posteriorly straight and medially from stomach, passing under ventricle, then turning upwards and entering ventricle without any coiling or loop, passing behind heart over posterior adductor and on posterior side of adductor turning ventrally, anus at mid-diameter of adductor. Heart rather narrow, situated well posteriorly, its long auricles fused posteriorly just in front of posterior adductor, extending anteriorly in long and narrow lobes to midpoint of shell-mantle length.

Type Material: Holotype NIWA H.790 (pair, preserved in alcohol) and paratypes NMNZ M.154988 (5), NIWA P.1246 (7), MNHN (2), all from type locality; 24 May 2001, R/V *Tangaroa* (stn 107/230). Paratypes: Rumble III submarine volcano, S Kermadec Ridge, 35°44.47′

Figure 43. *Gigantidas gladius* new species in situ on Rumble III volcano, 386 m, 22 May 2001 (NIWA sta. TAN107/152). The largest mussels in the foreground at lower right and at top left centre are 250–300 mm long. The starfish is a new genus and species of the Astereidae (D.G. McKnight, pers. comm.). From color photograph taken by remote camera (courtesy NIWA).

Table 2. *Gigantidas gladius* new species. Shell measurements (mm) and proportions.

Length	Height	Tumidity	Length/height	Specimen
316.0	54.1	56.1	5.84	Paratype 1 NMNZ
288.0	46.7	43.2	6.17	Paratype 2 MNHN
271.3	44.0	45.3	6.16	Paratype 3 NMNZ (dissected)
270.0	56.6	48.5	4.77	Paratype 4 NMNZ (broken)
260.0	45.0	41.7	5.78	Holotype NIWA
253.5	47.0	41.7	5.39	Paratype 5 NMNZ (1 v broken)
247.8	44.8	40.6	5.53	Paratype 6 NIWA
245.5	43.1	40.2	5.69	Paratype 7 NMNZ
244.3	45.2	44.0	5.40	Paratype 8 NIWA
231.2	42.3	39.2	5.46	Paratype 9 MNHN
216.5	41.0	40.2	5.28	Paratype 10 NIWA
206.5	44.1	39.7	4.65	Paratype 11 NMNZ

S, 178°29.4′ E, alive, 216–460 m, 2 Nov. 2000, RV Kaharoa (many juveniles: NMNZ M.158285, NIWA P.1248, KAH11/21, MNHN).

Type Locality: Rumble V submarine volcano, southern Kermadec Ridge off northeastern North Island, New Zealand, 36°08.48′ S, 178°11.70′ E, 733–360 m.

Other Material Examined: Rumble III, 238–350 m, 2 Nov. 2000, RV Kaharoa (many small to moderate-sized specimens, NIWA P.1249; KAH11/22); RV Kaharoa (36 pairs, NIWA P.1250; KAH11/12); 382–207 m, 19 May 2001, RV Tangaroa (51 pairs, NIWA TAN107/002); 420–220 m, 19 May 2001, RV Tangaroa (78 pairs, NIWA TAN107/005); 420–230 m, 23 May 2001, RV Tangaroa (253 pairs, NIWA TAN107/216); Rumble V, 755–360 m, 24 May 2001, RV Tangaroa (103 pairs, NIWA TAN107/230); 730–470 m, 24 May 2001, RV Tangaroa (27 pairs, NIWA TAN107/324); 485–415 m, 24 May 2001, RV Tangaroa (90 pairs, NIWA P.1247; TAN107/325).

Table 3. Polychaete worms (*Branchipolynoe* sp.) associated with *Gigantidas gladius* new species.

Shell length	Worm length	Location of worm within mussel, and pathology
316.0 mm	35 mm	In front of foot between right ctenidium demibranchs
288.0 mm	15 mm	Below posterior adductor
271.0 mm	39 mm	Anterior half with one end at mid-shell length
270.0 mm	30 mm	Ventral side of foot (lesions on ctenidia both sides)
260.0 mm	35 mm	Posterior end. Worm's posterior against posterior adductor
253.5 mm	40 mm	Right side between byssus and ctenidia (lesions on ctenidia both sides)
248.0 mm	34 mm	Between anterior tip of foot and anterior adductor
	9 mm	Beside the adult worm
244.0 mm	37 mm	Hind end at mid-shell length, head posterior
245.5 mm	30 mm	Near mouth, with head touching palps (lesion)
231.0 mm	34 mm	Between tip of foot and anterior adductor (lesion on right mantle edge)
216.5 mm	31 mm	In opening above mouth, about 15 mm of worm projecting posteriorly
206.5 mm	23 mm	Above ctenidia on right side at byssus level

Distribution (Figure 42): Submarine volcanoes, Kermadec Ridge, NE New Zealand, 216–755 m, shallowest occurrence unclear (obtained by dredging upslope), though certainly as shallow as 350 m.

Biotope: High population densities at sulphur-rich hydrothermal springs on active submarine volcanoes (Figure 42). Dredge hauls containing this mussel included elemental sulphur and smelled strongly of it, suggesting that the mussel's nourishment involves chemosynthesis by sulphur-oxidizing symbiotic bacteria concentrated in the extremely enlarged gills.

Etymology: So named because of its blade-shaped valves (Latin).

Remarks: *Gigantidas gladius* is currently the second largest living mytilid known, being only slightly surpassed in length by *Bathymodiolus boomerang* (shell length 316 mm, vs. 370 mm). *Bathymodiolus boomerang*, however, is a true *Bathymodiolus* species with a siphonal membrane and a posterior retractor with only two muscle bundles, and is much higher posteriorly, and more strongly curved anteriorly. Other major distinguishing characteristics of *G. gladius* are the attachment of the anterior retractor well in front of the umbonal cavity directly above the anterior adductor, rather than somewhere within the umbonal cavity as in *Bathymodiolus* species, and the uniting of the anterior adductor and retractor scars, which are separate in *Bathymodiolus* species.

All 11 intact adult type specimens of *G. gladius* contained a polychaete of the genus *Branchipolynoe*. On opening the mussels, the worm was found situated at various sites within the mantle cavity (Table 3), some causing lesions on the mantle edge or in the mouth region. One mussel even had a worm projecting from the opening into the dorsal mantle cavity above the mouth. Thus the mussel is often traumatized by the polychaete (Britayev et al., 2001).

ACKNOWLEDGMENTS

We are grateful to Steve O'Shea and Malcolm Clark, National Institute of Water and Atmospheric Research, Wellington, for loan and gift of material, to Malcolm Clark for the *in situ* photograph, and to his co-workers Keith Lewis and Ian Wright for information on geology of collecting sites, and Richard Garlick for the distribution maps. The specimens of *Gigantidas gigas* were obtained in connection with the following programs funded by the New Zealand Foundation for Research, Science and Technology: "Seamounts: importance to fisheries and marine ecosystems" (C01X0028), and "Consequences of earth ocean change" (C01X0203). Two anonymous referees are thanked for helpful comments on the manuscript.

LITERATURE CITED

Britayev, T. A., E. M. Krylova, R. von Cosel, D. Martin and T. S. Aksnik. 2001. The association of giant mussels, *Bathymodiolus* spp., with scaleworms, *Branchipolynoe* aff. *seepensis* (Polychaeta: Polynoidae): commensalism or parasitism? International Conference on Polychaeta, Reykjavik, July 2001, Programme and Abstracts: 29.

Childress, J. J., C. R. Fisher, J. M. Brooks, M. C. Kennicutt II, R. Bidigare and A. E. Anderson. 1986. A methanotrophic marine molluscan (Bivalvia, Mytilidae) symbiosis: mussels fuelled by gas. Science 233: 1306–1308.

Cosel, R. von. 2002. A new species of bathymodioline mussel (Mollusca: Bivalvia: Mytilidae) from Mauritania, West Africa, with comments on the genus *Bathymodiolus* Kenk & Wilson, 1985. Zoosystema 24: 259–271.

Cosel, R. von, T. Comtet and E. M. Krylova. 1999. *Bathymodiolus* (Bivalvia: Mytilidae) from hydrothermal vents on the Azores Triple Junction and the Logatchev hydrothermal field. Mid-Atlantic Ridge. The Veliger 42: 218–248.

Cosel, R. von, B. Métivier, B. and J. Hashimoto. 1994. Three new species of *Bathymodiolus* (Bivalvia: Mytilidae) from hydrothermal vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit area, Mid-Atlantic Ridge. The Veliger 37: 374–392.

Cosel, R. von and K. Olu. 1998. Gigantism in Mytilidae: A new *Bathymodiolus* (Mollusca: Bivalvia) from cold-seep areas on the Barbados Accretionary Prism. Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Vie 321: 655–663.

Dell, R. K. 1987. Mollusca of the Family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzen-

berg, 1927 and *Idasola* Iredale, 1915. Records of the National Museum of New Zealand 3: 17–37.

Dell, R. K. 1995. New species and records of deep water Mollusca from off New Zealand. Tuhinga. Records of the Museum of New Zealand Te Papa Tongarewa 2: 1–26.

Fisher, C. R., J. J. Childress, R. S. Oremland and R. R. Bidegare. 1987. The importance of methane and thiosulfate in the metabolism of the bacterial symbionts of two deep-sea mussels. Marine Biology 96: 59–71.

Gustafson, R. G., R. D. Turner, R. A. Lutz and R. C. Vrijenhoek. 1998. A new genus and five new species of mussels (Bivalvia: Mytilidae) from deep-sea sulfide/hydrocarbon seeps in the Gulf of Mexico. Malacologia 40: 63–112.

Hashimoto J. and M. Horikoshi. 1989. A burrowing species of "*Bathymodiolus*". Deep-Sea Newsletter 15: 32–34.

Hashimoto, J. and T. Okutani. 1994. Four new mytilid mussels associated with deepsea chemosynthetic communities around Japan. Venus 53: 61–83.

Kenk, V. C. and B. R. Wilson. 1985. A new mussel (Bivalvia: Mytilidae) from hydrothermal vents in the Galapagos Rift zone. Malacologia 26: 253–271.

Lewis, K. B. and B. A. Marshall. 1996. Seep faunas and other indicators of methane-rich dewatering on New Zealand convergent margins. New Zealand Journal of Geology and Geophysics 39: 181–200.

Nelson, D. C., K. D. Hagen and D. B. Edwards. 1995. The gill symbiont of the hydrothermal vent mussel *Bathymodiolus thermophilus* is a psychrophilic, chemoautotrophic, sulfur bacterium. Marine Biology 121: 487–495.

Parson, L. M. and I. C. Wright. 1996. The Lau-Havre-Taupo Back-arc Basin: a southward, propagating, multi-stage, evolution from rifting to spreading. Tectonophysics 263: 1–22.

Rio, M., M. Roux, M. Renard and E. Schein. 1992. Chemical and isotopic features of present day bivalve shells from hydrothermal vents or cold seeps. Palaios 7: 351–360.

Ronde, C. E. J. de, E. T. Baker, G. J. Massoth, J. E. Lupton, I. C. Wright, R. A. Feeley, and R. R. Greene. 2001. Intra-oceanic subduction—related hydrothermal venting, Kermadec volcanic arc, New Zealand. Earth and Planetary Science Letters 193: 359–369.

Tunnicliffe, V. 1991. The biology of hydrothermal vents: ecology and evolution. Oceanography and Marine Biology Annual Review 29: 319–407.

Wright, I. C. 1994. Nature and tectonic setting of the southern Kermadec submarine arc volcanoes: an overview. Marine Geology 118: 217–236.

Wright, I. C. 1997. Morphology and evolution of the remnant Colville and active Kermadec arc ridges south of 33°30′ S. Marine Geophysical Researches 19: 177–193.